Risk of brown bear predation on semi-domesticated reindeer calves

Predation patterns, brown bear – reindeer interactions and landscape heterogeneity

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Cover: Reindeer calf in Udtja reindeer herding district
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Abstract

As large carnivore populations are recovering in northern boreal ecosystems of Europe and North America, there is a need to understand how these changes in predator communities influence prey populations and ecosystems. Moreover, human-wildlife conflicts are frequently causing challenges where large carnivores coexist with humans, often due to predation on livestock. In Sweden the brown bear (*Ursus arctos*) distributional range largely overlaps with the reindeer (*Rangifer tarandus tarandus*) herding area, but knowledge of potential losses to bear predation has been scarce. Also, little information exists on the behavioral interactions between semi-domesticated reindeer and brown bears in Fennoscandia. In this thesis I present data from two forest reindeer herding districts in Northern Sweden, showing that brown bear predation on reindeer neonates can be considerable on forested calving grounds. Also, brown bear predation was very limited in time, concentrated to the first weeks following birth of the reindeer calves. Moreover, using GPS location data to compare brown bear and reindeer resource selection on the reindeer calving ground, indicated that brown bear behavioral adjustments to search for reindeer possibly dominate over antipredator responses by reindeer in terms of altered resource selection on a daily and seasonal basis. Nevertheless, a closer investigation of the spatial distributions of reindeer calf kill sites suggested that use of clear-cuts, higher elevations and areas closer to large roads may reduce risk of bear predation. However, even though clear-cuts may provide advantages for survival in the short term, logging may eventually yield negative effects for the reindeer, as abundance of young forest increase, which is a preferred habitat by brown bears. Finally, using data on reindeer movements and brown bear density from seven herding districts in Sweden I show that reindeer females experiencing higher risk of bear predation, deviate more from optimal foraging and increase movement rates, which may lead to lower body condition and, in turn, possible consequences for population dynamics.

Keywords: Rangifer, brown bear, predation, landscape characteristics, habitat selection, antipredator behavior, green wave

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Dedication

Til Heming og Nokve

We do not inherit the earth from our ancestors; we borrow it from our children
Ancient proverb

Contents

List of publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I Støen O-G, Sivertsen TR, Rauset GR, Kindberg, J, Bischop, R, Skarin A, Segerström P and Frank J. Brown bear predation on neonatal semi-domestic reindeer: patterns and possible mitigations (*manuscript*)

II Sivertsen TR*, Åhman B, Steyaert SMJG, Rönnegård L, Frank J, Segerström P, Støen O-G and Skarin A. (2016) Reindeer habitat selection under the risk of brown bear predation during calving season. *Ecosphere* 7(11): e01583

III Sivertsen TR, Skarin A, Rönnegård L, Åhman B, Frank J, Segerström P and Støen O-G. Brown bear predation on semi-domesticated reindeer calves: relating kill locations to landscape heterogeneity (*manuscript*)

IV Rivrud IM**, Sivertsen TR**, Mysterud A, Åhman B, Støen O-G and Skarin A. Reindeer green-wave surfing constrained by predators (*manuscript*)

Paper II is published with open access.

* Corresponding author.

** These authors contributed equally to this work

The contribution of Therese R. Sivertsen to the papers included in this thesis was as follows:

I Participated in the planning of the work together with OGS, JF and PS. Contributed to idea and hypothesis. Participated in the field work and collection of data. Performed a substantial part of the analyses and compilation of results. Contributed significantly to the writing of the manuscript (main author O-G Støen).

II Designed the study, and formulated idea and hypothesis, together with AS, BÅ, LS and OGS. Performed a majority of the field work and collection of data. Performed the analyses and compiled the results. Wrote the manuscript with support from the co-authors, and acted as corresponding author towards the journal.

III Designed the study, and formulated idea and hypothesis, together with AS, BÅ and LS. Performed a majority of the field work and collection of data. Performed the analyses and compiled the results. Wrote the manuscript with support from the co-authors.

IV Participated in designing the study, and formulating idea and hypothesis, together with IMR, AS, O-G and AM. Contributed to idea and hypothesis. Participated in the collection of data. Performed all preparation of data, and contributed to analysis. Wrote the manuscript together with IM Rivrud (shared first author), with support from the other co-authors.

1 Introduction

Reindeer herding forms a basis for the Sámi cultural heritage. The land devoted to reindeer herding in Sweden covers more than half of the total land area (Sandström 2015). Owing to successful conservation efforts, populations of large carnivores have increased rapidly in Fennoscandia over the last century (Chapron *et al.* 2014). Whereas there is a management goal to sustain viable populations of large carnivores across Fennoscandia, Sweden have also committed to ensure the livelihood of the Sámi people, including a sustainable reindeer husbandry (Nilsson-Dahlström 2003). Direct losses of semi-domesticated reindeer to predation can be substantial, and depredation of reindeer causes both economical and emotional strain for the reindeer herders.

The brown bear distributional range largely overlaps with the reindeer herding area in Sweden. However, knowledge so far is scarce about the impacts of brown bear predation on semi-domesticated reindeer populations. Brown bears are generally known to be efficient predator on ungulate neonates (Linnell, Aanes & Andersen 1995; Nieminen 2010), and can impose a major limiting factor on *Rangifer* (i.e. caribou and reindeer) population growth (Adams, Singer & Dale 1995). Moreover, integration of landscape heterogeneity in the understanding of large mammalian predator-prey interactions is experiencing increased focus. This includes identifying landscape structures that increase predation risk or prey safety, estimating the indirect costs in a prey population caused by behavioral adjustments to predation risk, and estimating possible consequences of landscape changes on predator-prey behavioral interactions.

Improved knowledge of brown bear predation on semi-domesticated reindeer calves, and the predator-prey behavioral interactions in these systems, can help us better predict the impact from brown bear predation on semi-domesticated reindeer populations. It can thus aid in making informed and evidence-based management decisions, and contribute to an increased understanding of *Rangifer* - large carnivore interactions.

1.1 Reindeer husbandry in Sweden

Reindeer husbandry represents an essential part of the Sámi culture and livelihood. Although it is a small industry on a national scale, it has great economic importance for local communities. The "Swedish Reindeer Herding Act" secures pastoral reindeer herding as an exclusive right for the Sámi people (Torp 2013). During the last decade, the number of semi-domesticated reindeer in Sweden has varied around 250 000 animals. Reindeer herding takes advantage of the natural adaptation of the species to a boreal/sub-arctic/arctic environment, and depends on large areas and high flexibility in land use to sustain productivity of the herd (Roturier & Roué 2009). The reindeer husbandry area in Sweden covers approximately 50 percent of the land area, and is divided into 51 reindeer herding districts. Of these, 33 are mountain herding districts, 10 forest herding districts and eight concession herding districts (Fig. 1). The mountain districts have their winter ranges in the forest, and the calving and summer ranges in alpine areas, whereas reindeer in the forest districts remain in forested areas year-round. The concession herding districts engage in reindeer husbandry east of the Swedish Lapland border with special permission from the administrative board of Norrbotten County. Except for occasional gatherings throughout the year, the reindeer are mostly freely ranged within the borders of the herding district. The most important events during a "reindeer herding year" is the migration from the winter ranges to the calving grounds in early spring, gathering of the herd for calf marking in the summer, and gathering for slaughter, separation into winter groups and migration to the winter ranges in early winter. Climate change, loss of grazing land and disturbance caused by infrastructure development, and increasing predator populations cause challenges to reindeer husbandry (Pape & Löffler 2012). Currently, the Swedish scheme for compensation is a "compensation-in-advance" scheme (Schwerdtner & Gruber 2007) based on the risk of economic loss by herders. This risk is estimated from the number of predators present within the herding districts (Swenson & Andrén 2005). In 2016, reindeer herders received 52.8 million SEK for estimated losses to predation, where 1.6 million SEK represented losses to brown bear predation (Sami Parliament 2017).

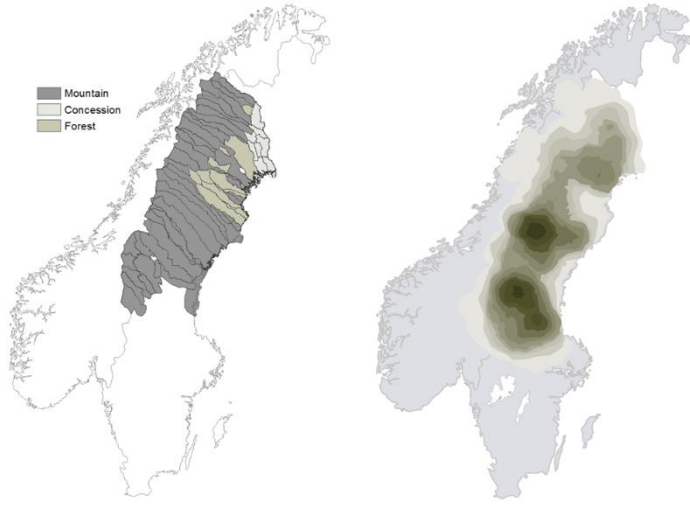

Figure 1. Maps showing the reindeer herding area in Sweden (left; source: iRENMARK - Sametinget, Sweden) and the brown bear distributional range in Norway and Sweden (right; darker color indicate higher bear densities, source: Scandinavian Brown Bear Research Project 2013)

1.2 *Rangifer* foraging ecology and antipredator behavior

The foraging behavior of *Rangifer* reflects the seasonality of the arctic and subarctic regions, with large variations in food availability throughout the year, but where the annual phenological succession of vegetation tends to be highly predictable (Skogland 1984). Generally, the diet composition of *Rangifer* depends on the nutrient contents, digestibility, amount of secondary compounds and relative availability of potential food (White & Trudell 1980; Skogland 1984). Throughout spring and summer, *Rangifer* favor plants of early growth phase that are high in nutrients. During the leafing and flowering stages alpine and arctic plants commonly have a high level of TNC (total non-structural carbohydrates) and nitrogen and only small amounts of cell wall elements of low digestible value (Skogland 1984).

In winter, *Rangifer* prefer to feed on lichens (Bergerud 1972; Skogland 1984; Danell *et al.* 1994; Kojola *et al.* 1995), and to a lesser degree on dwarf shrubs, mosses, sedges and grasses. Although poor in protein and most macrominerals, lichens are rich in soluble carbohydrates, which is an essential source of energy in the cold season, and due to low amounts of cellulose and lignin they are highly digestible (Klein 1990; Danell *et al.* 1994).

Rangifer commonly employ either a “space away” or a “space out” strategy to reduce predation risk during calving (Bergerud, Butler & Miller 1984; Bergerud & Page 1987; Seip 1991; Rayl *et al.* 2014). Some caribou populations in North America separate spatially from predation risk by migrating several hundred kilometers northwards to calve in areas above the tree line, thereby avoiding the high densities of predators that are present further south (Bergerud & Page 1987). Some *Rangifer* populations may space away from predators and alternate prey with shorter migratory movements to calving grounds in the mountains, on islands and along shore lines (Bergerud 1985; Bergerud & Page 1987). Forest – dwelling herds of woodland caribou typically persist at lower densities and space out during calving to increase searching time by predators (Bergerud & Page 1987; Seip 1991; Rayl *et al.* 2014), and also reduce predation risk by selecting habitats with lower encounter risk within the calving range (Rettie & Messier 2000; Mahoney & Virgl 2003; Pinard *et al.* 2012).

Predation risk may also drive fine-scale selection of calving sites within the calving grounds. *Rangifer* is a typical follower species, being mobile and following its mother shortly after birth (Vos, Brokx & Geist 1967). Because Rangifer neonates grow at a maximal rate, they quickly gain the ability to flee from predators (Parker et al. 1989). Hiding may nevertheless be important immediately after birth. Indeed, during the first 48 hours, reindeer calves may adopt a prone position to avoid detection from predators (Lent 1966). Shrub cover can obscure the visibility of the calves, making it harder for predators to detect them (Bowyer, Kie & Van Ballenberghe 1998; Gustine *et al.* 2006)**,** at the same time offering important spring forage for parturient females (Crête, Huot & Gauthier 1990). Also, *Rangifer* may choose calving sites at elevated locations for a better overview, and adjust the choice of slope directions according to the prevailing winds, to prevent the scent from reaching the predators (Bergerud et al. 1984, Gustine et al. 2006).

1.3 Brown bears in Sweden

The brown bear population in Sweden has increased from an estimated number of 294 bears in 1942, to 834 bears in 1993, reaching a maximum of 3298 individuals in 2008. The most recent population estimate from 2013 suggested a decline to 2782 individuals (Swenson *et al.* 2017). The brown bear distributional range covers approximately two thirds of the land area in Sweden, and brown bears are only absent from the most southern parts of the country (Fig. 1). Brown bears are hunted at annual quotas in Sweden. The hunting season is in the autumn (21 August – 15 October, or until quotas are reached).

Brown bears in Scandinavia are manly associated with forested areas at lower elevations (May *et al.* 2008; Støen *et al.* 2016). Brown bears hibernate, mainly from October to April (Linnell *et al.* 2000), and the mating season is during May and June (Dahle & Swenson 2003a). Their habitat use is largely driven by food availability, shelter opportunities, intraspecific interactions, and human avoidance (Moe *et al.* 2007; Martin & Basille 2010; Steyaert *et al.* 2013). Brown bears are generalist foragers with a broad diet, including various vegetation (e.g. grasses, sedges, herbs and berries), insects, and mammals (e.g. ungulates) (Mattson, Blanchard & Knight 1991; Dahle, Sørensen & Wedul 1998). The diet varies with availability and nutritional demands of the bears throughout the season (Mattson *et al.* 1991; Dahle *et al.* 1998). During the ungulate calving season (i.e., spring), ungulate neonates can be an important component of the brown bear´s diet (Mattson *et al.* 1991; Adams *et al.* 1995; Linnell *et al.* 1995; Nieminen 2010). Because brown bears are closely associated with forest habitat in Sweden, reindeer herding districts with their calving grounds located in the forest may be particularly vulnerable to brown bear predation.

2 Objectives

The aim of this thesis was to document brown bear predation patterns on semi-domesticated reindeer calves in Sweden, and to investigate the behavioral interactions of female reindeer and brown bears during the calving period. To increase understanding of the influence of brown bears predation on reindeer, the thesis evaluates individual brown bear kill rates on the calving range, reindeer and brown bear habitat selection patterns during calving, and the relation of kill site distribution to landscape characteristics in two forest reindeer herding districts in northern Sweden. Finally, on a broader scale, including seven herding districts, I investigated how the presence of brown bears may influence reindeer movement patterns and access to high quality forage. The main research questions were:

- Paper I: What are individual brown bear kill rates on the reindeer calving ground, and how do kill rates vary between individuals and over time? And further, how much of the total calf mortality in a herding district can be caused by brown bear predation?
- Paper II: What are the characteristics of female reindeer and brown bear habitat selection within the reindeer calving range, and how does selection patterns and spatial overlap vary on a daily and seasonal basis, relative to temporal variations in brown bear predation risk?
- Paper III: How does the spatial distribution of reindeer calf kill sites relate to landscape characteristics, and to the relative probability of reindeer habitat selection and reindeer-brown bear co-occurrence? Do fine-scale attributes of kill sites indicate effects of habitat on predation risk?
- Paper IV: Do reindeer have lower access to high quality forage, and higher and more variable movement speeds, at higher bear densities? And, is this response most pronounced during the peak predation period?

3 Methods

3.1 Study systems

3.1.1 Udtja and Gällivare reindeer herding districts

The study area in paper I - III was centered on the calving and post-calving ranges of Udtja (66.2° N,19.4 ° E) and Gällivare (66.6° N, 21.4 ° E) forest reindeer herding districts, located in Norrbotten County, northern Sweden. The borders of the study areas defined in paper I (Udtja: 1283 km^2, Gällivare: 2469 km^2; Fig. 2), and further used as the framework for paper II and III, was delineated by a combination of the reindeer herder`s definitions of the reindeer calving range, formal herding district borders, and landscape features (i.e. rivers, roads and railways). The area is part of the European taiga, and the forest is dominated by Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*), interspersed with bogs, lakes and at the highest elevations subalpine birch (*Betula pubescens*) forest. The topography is characterized by an undulating forested landscape with elevations ranging from 13 to 714 m a.s.l.

The human population is relatively low within the areas (average 0.02 per km^2) with few human settlements. The densities of small roads (mainly gravel roads) and major roads (public roads with regular traffic) were approximately 0.25 and 0.02 km/km^2 in Udtja, and 0.38 and 0.06 km/km^2 in Gällivare, respectively. The reindeer densities in Udtja and Gällivare were between 1.1-1.5 animals/km^2. Udtja spring and summer ranges are mainly located within a closed military missile range, with the main human activities in the area being military training actions. Since 1995, a large part of the area is also a nature reserve with no logging activity allowed. In Gällivare, logging activities are more intense and road density is higher. In both districts, reindeer move freely within the district borders, and are subject to herding activities. The district

borders follow reindeer fences, rivers, roads and railroad tracks, which support reindeer herders to separate their herds, but do not constitute impassable barriers for wildlife. In Udtja in particular, seasonal movements by the reindeer from the winter areas to the calving ranges correspond to the elevation range following a south-north gradient, with higher elevations in the north.

Prior to the study the two reindeer herding districts claimed losses of calves to bear predation. The brown bear population in Norrbotten was estimated to 713-1152 individuals in 2011 (Tyrén 2011). Bears are hunted during the annual hunting season in the autumn (21 August - 15 October or until quota are filled). In Udtja and Gällivare, the estimated brown bear population size in 2010 was 62-96 and 53-75 individuals, respectively. Wolves are absent in the study area and population densities of lynx and wolverines are low (Tyrén 2011).

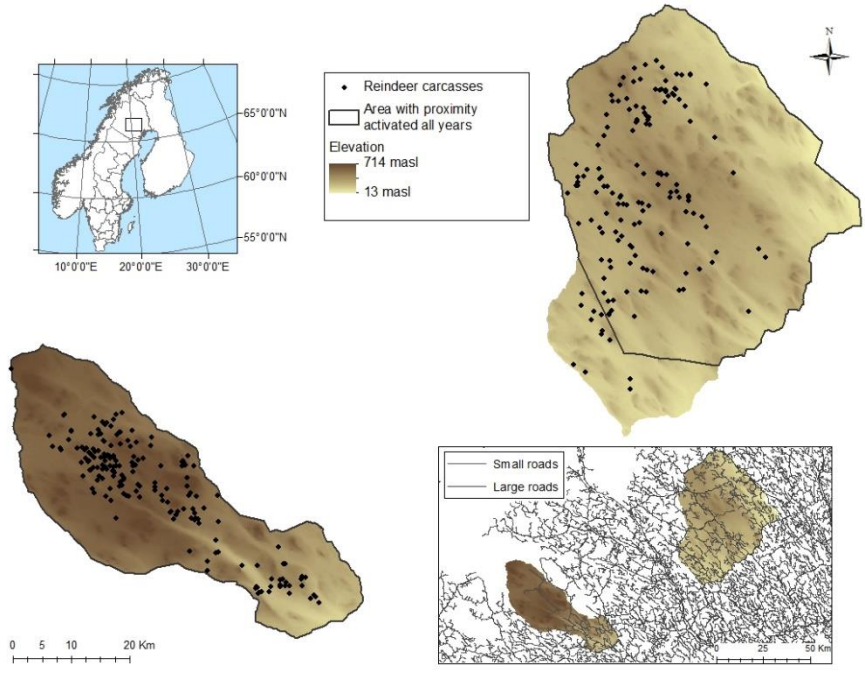

Figure 2. The study area in paper I - III, located on the calving and post-calving ranges in Udtja and Gällivare forest reindeer herding districts. The proximity function in the brown bear GPS-collar was turned on when the bear was inside the defined borders of the study areas. The colored areas indicate the study areas in 2012 and the black line indicate the range where the proximity function in the brown bear GPS collars was activated all years of the study period. Black dots represent all reindeer carcasses documented killed by brown bears during the study period 2010-2012.

3.1.2 Herding districts in paper IV

In paper IV, locational data from reindeer was collected from four forest herding districts (Gällivare, Malå, Udtja and Östra Kikkejaure) and three mountain herding districts (Handölsdalen, Njaarke and Sirges), within the reindeer husbandry range in Sweden. The calving- and post-calving ranges of the forest herding districts are all characterized by undulating boreal forests interspersed with mires and lakes. Active forestry occurs in all forest districts apart from within the nature reserve in Udtja. The mountain district calving ranges are all located in the mountain region and mainly above the tree line.

3.2 GPS and predation data

3.2.1 Collaring of reindeer and brown bears in Udtja and Gällivare

From 2010-2012 in Udtja and 2011-2012 in Gällivare, the majority of adult reindeer females in the study populations were equipped with proximity UHF-collars (Udtja 2010:990, 2011:1176, 2012:1235; Gällivare 2011:893, 2012:1350), and 24 brown bears with GPS collars containing UHF receivers (Vectronic Aerospace GmbH, Berlin, Germany) of which 21 bears (Udtja 2010:4, 2011:7, 2012:8; Gällivare 2011:4, 2012:8) were tracked within the calving ranges, with the proximity function activated (see explanation further down). Also, a total of 97 individual reindeer females (Udtja 2010:19, 2011:29, 2012:25; Gällivare 2011:16, 2012:21) were GPS-collared, these were mainly so-called “leading females”, considered to be most representative for the herd movements. The GPS was scheduled to take a location every 2 hours (Telespor AS, Tromsø, Norway; Followit AB, Stockholm, Sweden).

All reindeer females equipped with a proximity collar were documented to be pregnant. Pregnancy status of female reindeer was determined using a rectal ultrasound probe in late March or early April. The reindeer UHF proximity collars emitted a weak UHF signal every second that could be detected by the brown bear GPS collars within the proximity of up to 100 m. The brown bear GPS collars were programmed to scan for UHF signals from the reindeer collars for 1.5 s every 8 s. Every time a UHF signal was detected, the GPS positioning schedule was altered from the standard 30-min schedule to one GPS position every 1 min and 10 s. This 1-min schedule persisted for one hour after the UHF signal was detected, and if new signals were received within this period, it lasted until 1 h after the last UHF signal. The GPS-collar sent an Iridium satellite message with the GPS locations to a database several times per day. With no Iridium coverage, the GPS locations were stored and sent at the

next possible occasion. The proximity function of the bear collars was activated when the bears were within the study areas during the period from 26 April to 24 September annually.

3.2.2 Documentation of reindeer carcasses in Udtja and Gällivare

During 2010, all 1-min GPS locations by brown bears were visited, but since no calf carcasses were found on tracks or clusters of minute locations with less than four GPS location within a 30 m radius, only clusters with ≥ 3 1-min GPS locations within a 30 m radius were visited in 2011 and 2012. At a kill cluster, reindeer carcasses were classified according to age (calf, adult) and sex (male, female). We estimated the time of death based on carcass decomposition and other signs (e.g. in snow or vegetation) to decide whether the calf was killed by the GPS collared bear, or by other causes. The conclusion of mortality cause was determined by consensus, following the standards for provincial rangers (Skåtan & Lorentzen 2011) (Fig. 3). All clusters were inspected by one researcher and one reindeer herder. If clusters from several bears were overlapping in time on a kill site, the bear with the first GPS position at the kill site were judged to have killed the reindeer, unless the GPS 1-min locations gave clear indications that a another bear likely was responsible for the kill.

Figure 3. Remains of a reindeer calf killed by a brown bear in Gällivare reindeer herding district. Photo: Therese R. Sivertsen

3.2.3 Processing of GPS and kill site data for paper II-IV

All reindeer GPS data were checked manually for obvious errors, and by the method of Bjørneraas et al. (2010). Brown bear data was automatically screened to remove location outliers when downloaded from the collar, and were also checked manually upon inclusion in analyses.

To estimate resource selection functions in paper II and III, we used reindeer and brown bear location data located inside the 100% minimum convex polygon (MCP) encompassing all reindeer GPS positions within the predefined study area in paper I, from 10 May – 30 June. The data encompassed 110 adult female reindeer years and 29 brown bear years, representing 97 individual reindeer females (Udtja:67; Gällivare:30) and 19 individual brown bears (Udtja:11; Gällivare:8).

The reindeer GPS data representing seven herding districts in paper IV included totally 557 542 locations from 319 GPS-collared reindeer females, collected in 2003 and from 2008 to 2015, covering the calving period (11 May - 9 June) and post-calving period (10 June - 31 August). The individual home ranges corresponding to the two sub-periods were estimated by calculating 95 % adaptive Local Convex Hull (a-LoCoH) polygons using the "adehabitatHR" package in R (Calenge 2006, R Core Team 2016).

To analyze the spatial distribution of kill sites, we used all kill sites within the area where the brown bear proximity collars had been activated during all years of study (Fig. 2), and where we had brown bear and reindeer locational data. To avoid pseudo replicates in our analyses we removed one kill site by random when two sites were < 50 m apart (totally 13 sites removed), resulting in totally 305 kill sites (Udtja: 178; Gällivare: 127).

3.3 Environmental data

3.3.1 Landscape characterstics in paper II, III and IV

The landscape parameters included in the resource selection models in paper II and III were extracted using Arc GIS 10.0-10.3 software (ESRI Inc., Redlands, California, USA ©2010–2015). Land cover classes included coniferous moss forest, coniferous lichen forest, deciduous forest (included in "other"-category in Gällivare, paper III), wetland, other open habitats, recent clear-cuts (0-5 years), old clear-cuts (6-12 years, or < 2 m height in the year 2000) and young forest (2-5 m height in the year 2000). Clear-cuts were merged to one category in Udtja in paper II, and for both districts in paper III. In addition we included elevation from a digital elevation model (DEM) 50 m in grid size, terrain

ruggedness (VRM, neighborhood parameter set to five cells; Sappington et al. 2007) calculated from DEM, and minimum Euclidean distance to the nearest large road (public road with regular traffic) and small road (typically gravel roads) roads. Large roads were not included in Udtja, due to a skewed distribution and correlation with elevation. We transformed distance to road using $1 - e^{\alpha d}$ (d=distance to feature, α was set to 0.002, approximate effect zone < 1500 m), resulting in exponential decays ranging from 0, to 1 at very large distances (Nielsen, Cranston & Stenhouse 2009). The final map was rasterized into a 50 m grid.

In paper IV, maps of terrain ruggedness were made with R "raster package" (Hijmans & van Etten 2015), and slope and aspect using ArcMap 10.3.1, all derived from the DEM model. Aspect was converted to "northness" (cosine transformed) ranging from -1 (south) to 1 (north). Maps were rasterized with a resolution of 100 m.

All digitized geographical data were provided by Lantmäteriet (www.lantmateriet.se), land cover data was obtained from vegetation vector maps, the Swedish Land cover Map 25 × 25 m (SMD Corine Land Cover Data 2000) and satellite image forestry data ("Utförd avverkning", Swedish Forest Agency 2015).

3.3.2 Fine scale registrations in paper III

In paper III, we recorded fine-scale habitat characteristics at totally 142 kill sites and 126 control sites from 13 May to 9 June in 2012 within Udtja and Gällivare herding districts. Control sites represented sites used by bears in close vicinity to reindeer females during this period, but where no kill had occurred in instant distance or time ("encounters"; first bear GPS minute location after proximity function activation, minimum 200 m and 5 min from a known kill). We registered land cover within a 20 m radius of the kill, distance to visible habitat edge, snow depth and cover, and sightability based on i) average distance to closest visual obstructions measured with a range finder sitting in knee height in each cardinal and one random direction, and ii) distance to walk until we lost site of the 30 m high lower section of a collapsible cover cylinder, 60 cm high and 30 cm in diameter (Ordiz *et al.* 2009).

3.3.3 Plant phenology in paper IV

Plant phenology was quantified using the satellite-derived normalized difference vegetation index (NDVI; Pettorelli et al. 2005) derived from

250x250m satellite images taken every 16 days and downloaded from the NASA Land Processes Distributed Active Archive Center (LP DAAC 2000) website. By fitting a double logistic curve to each pixels annual NDVI time series, the instantaneous rate of green-up (IRG) can be extracted by taking the first derivative of the part of the curve that covers spring (Bischof *et al.* 2012). By using reindeer female GPS location data and calculating the cumulative IRG (CIRG) for each reindeer individual, we could get a measure of the total amount of high quality forage experienced by the individual (Bischof *et al.* 2012).

3.3.4 Bear density index in paper IV

Bear density in the home ranges of reindeer females was estimated from the latest scat survey (non-invasive DNA) conducted in each County (www.rovbase.no, Bellemain et al. 2005, Kindberg et al. 2011). We used all bear scats where the individual bear had been identified and calculated scat density with the density tool and 1000 m resolution in ArcGIS (ESRI 2015).

3.4 Brown bear predation on reindeer calves

3.4.1 Seasonal kill rate model

We used the registered number of reindeer calves killed by individual GPS-collared bears within Udtja and Gällivare study areas to estimate kill rate as a function of bear demographic category. Because the collaring of female reindeer and registrations of kills were restricted to the defined study areas, whereas bears also stayed outside these borders, we accounted for individual differences in exposure time, using hours each bear spent within the study areas as an offset variable, log transformed to match the logit link function of the models. Alternative classifications were compared, as well as inclusion of herding district, and the best model chosen using AICc. We employed zero-inflated negative binomial models to account for over-dispersion and enable modelling of count data with more zeroes than expected from the Poisson distribution (Zeileis, Kleiber & Jackman 2008). This model was suitable to handle our data where several bears were not registered to kill any calves. It includes two separate processes; one part to model excess zeros, represented by a binomial GLM with a logit link, and a count part to model over-dispersed count outcomes, represented by a negative binomial GLM with a logit link (Zeileis *et al.* 2008). Here, the zero-part thus quantify the effects of variables affecting the probability of killing zero calves, and the count-part estimates the

number of reindeer calves killed by a bear per season (potentially corrected by the binomial part). Females with cubs of the year (FCOY) were not registered to kill calves, and were included in the binomial part, and the other demographic groups in the count part of the models. Since the frequency of repeated individual measurements was relatively low in our data set (n=8), we considered it justified to ignore the variation caused by repeated individual measurements in this model. To fit the model, we used the *zeroinfl()* function in the *pscl* package, version 1.4.9 in R (Jackman 2015). For model predictions, we calculated kill rates with "exposure time" from 0 to 991 hours (maximum observed value), divided into 100 intervals, and bootstrapped confidence intervals with 1000 replicates.

3.4.2 Between kill interval model

To calculate between kill intervals, we only used intervals between successive kills when the bear had resided within the defined calving range the entire time of the interval. Since the distribution of intervals was right-skewed, we used log-transformed time (minutes) between kills as a response variable in linear mixed effects models, using R package lme4 (Bates *et al.* 2015). As the distribution of kills throughout the year showed a distinct peak during late May, we included "day/week of year" as potential covariates, both as first and second order, in addition to the same demographic groups of bears as used for seasonal kill rates. Females with cubs of the year was not included. To account for potential individual effects and repeated observations, we tested combinations of year, herding district and bear individual as random intercepts. Bear individual was the only random effect included in the final candidate model set. The same principles as described for seasonal kill rates were used for model selection and predictions.

3.4.3 Estimation of total bear-caused calf mortality in Udtja and Gällivare

The total calf mortality caused by brown bears in Udtja and Gällivare reindeer herding districts was estimated from i) average number of bears within demographic categories expected to have home ranges overlapping with the calving ranges, ii) total calf mortality within the herding districts and iii) expected seasonal kill rate for demographic categories of brown bears.

The average number of bears was determined and classified to sex from scat collection and DNA sampling within a 19.7 km buffer of the study areas, corresponding to the mean radius of the GPS-collared bear's home ranges.

To estimate the total mortality of reindeer calves among adult reindeer females in the two study populations, female:calf ratios were registered by visual observations during summer calf marking (late June to mid-July) in the herding districts, when the females and calves are rounded up in corrals.

We then used the category specific effect sizes of the best kill rate model to predict the total number of calves killed on the calving ground, based on average time spent by GPS-collared bears inside the study area, and the estimated total number of bears and demographic classifications. Finally, we calculated the proportion of total calf mortality that was caused by bear predation, by comparing this number to the estimated total calf mortality in the two study areas.

3.5 Habitat and movement models

All statistical analyses were done in program R (R Core Team 2016). For linear mixed-effect models the package "lme4" (Bates *et al.* 2015) in R was employed.

3.5.1 Time periods in paper II and III

In paper II and III we restricted the study period to 10 May until 30 June. The focus was thus on the main predation period on reindeer neonates, and the succeeding period after predation ceased, before the reindeer were gathered for calf marking in early summer. Based on information from paper I, we subdivided the study period into the predation period (10 May – 9 June; 332 out of 335 calves were killed in this time interval) and the post-predation period (10 – 30 June). Further, we classified data into high predation hours (6 PM to 6 AM) and low predation hours (6 AM to 6 PM) within the predation period, based on findings of diurnal brown bear predation patterns in paper I.

3.5.2 Resource selection functions

Resource selection functions (RSFs), estimated using logistic regression and a use-availability design, is a well - established method in habitat selection studies (Johnson *et al.* 2006). We employed binary logistic regression (Lele & Merrill 2013) to estimate resource selection functions for reindeer and brown bears on the reindeer calving range (paper II), and the distribution of kill sites relative landscape characteristics (paper III). In paper II the binomial response represented reindeer and brown bear GPS locations versus an equal number of random location for each individual distributed within the two calving ranges,

respectively. The models included the environmental variables land cover, elevation, terrain ruggedness, distance to nearest road, and the interaction term time period as fixed factors, which made it possible to compare the selection patterns in relation to temporal variation in brown bear predation risk on a seasonal (predation/post-predation) and daily (high/low predation hours) basis. Using a model selection approach based on AICc and parsimony (Arnold 2010), we determined the best performing models for reindeer and brown bear resource selection. We also checked if the models explained more variation than the null-model, based on AICc. The best models were then validated using *k*-fold cross validation, following the approach of Boyce et al. (2002). In paper III, we employed the same set of covariates found to be important for reindeer and brown bear resource selection, to evaluate the spatial distribution of kill sites relative to random locations using resource selection functions. Here, the binomial response was kill sites versus random sites, ten times the number of kill sites, to make the analysis more robust. In all models, generalized linear mixed models were used, to account for repeated measurements across individuals (Zuur *et al.* 2009).

3.5.3 Spatial overlap between brown bears and reindeer

In paper II, we used predicted values from the RSFs to further investigate the spatial overlap between brown bear and reindeer female resource selection in relation to temporal variation in brown bear predation risk, on a seasonal and daily basis. We determined the level of spatial autocorrelation within the RSF maps using Gaussian-fitted semivariograms and considered the average semivariogram range of the RSF maps as the distance in which locations become spatially independent (see Hiemstra et al. 2009 for detailed description of theory and methodology). Based on this distance we generated a set of random locations in each study area, and extracted RSF- values for each species-time period combination. Pearson product moment correlation was then used to quantify correlation between reindeer and bear RSF values within the respective time periods.

3.5.4 Relative probability maps and weighted RSF models

In paper III, we used the best reindeer and brown bear RSF models from paper II, to estimate predictive maps with relative probability of reindeer habitat selection and reindeer – brown bear co-occurrence on the calving range during the predation period. We calculated relative probability for reindeer and brown bear selection for each 50 × 50 m grid cell from the model parameter estimates,

but dropped the fixed and random intercepts (Polfus, Hebblewhite & Heinemeyer 2011):

$$w(x) = \exp(\beta_1 x_1 \ldots + \ldots \beta_n x_n) \quad (1.)$$

where $w(x)$ is the relative probability of selection and β_n is the estimated coefficient for covariate x_n (Manly et al. 2002). Following the procedure of Courbin et al. (2009), we then used $w(x)$, and the smallest (w_{min}) and largest (w_{max}) RSF values for each model, to scale predicted RSF-values between 0 and 1:

$$\hat{w} = \frac{w(x) - w_{min}}{w_{max} - w_{min}} \quad (2.)$$

Finally, we calculated the relative probability of brown bear and reindeer co-occurrence $\hat{w}_{co}$:

$$\hat{w}_{co} = \hat{w}_{reindeer} \times \hat{w}_{brown\ bear} \quad (3.)$$

where $\hat{w}_{reindeer}$ and $\hat{w}_{brown\ bear}$ is the relative probability of selection in each 50 × 50 m grid cell for female reindeer and brown bear, respectively.

Then, to investigate the relation between kill site distribution, and reindeer habitat selection and co-occurrence probability, we sampled random points within the study area weighted by $\hat{w}_{reindeer}$ or $\hat{w}_{co}$ for each 50 × 50 m raster cell, and used these to estimate resource selection functions for kill site distribution, as described above. If the distribution of kill sites were proportional to the relative probability of reindeer habitat selection or reindeer-brown bear co-occurrence, no significant effects would be present in the model, whereas significant effect for a given landscape characteristic indicated a difference in kill probability relative to the likelihood of reindeer habitat selection or reindeer-brown bear co-occurrence for this covariate.

3.5.5 Fine – scale analysis of kill sites

Binomial logistic regression was used to compare fine-scale habitat characteristics between kill sites and control sites in paper III. Due to a small

sample size, we reduced the degrees of freedom in the models and merged land cover into “open”, “semi-open” and forest habitat. Edge was defined as a distinct visible edge between these categories and divided into four categories (“0-10 m”, “11-50 m”, “>50 m” and “no visible edge”). To avoid inclusion of extreme distances in the sightability index, 100 m was set as the maximum limit. To avoid a temporally unbalanced sample, we identified the break-point when predation decreased, and randomly removed control sites after this date so that the number of kills and control were equal. We made a snow index by multiplying mean snow depth with snow cover. We pooled data across study areas and if sites were < 50 m apart, one site was removed by random. Because sightability and snow conditions change over the season, we restricted inclusion of sightability measures within seven days after the true date, and only included snow measurements taken before the accumulated snow index was 99 %. Due to different number of observations for the covariates, we tested models separately (using AICc and compare to null-model) within each data set; “distance to edge” (kill=142, control=126), “sightability” (kill=142, control=83), and “snow” (kill=108, control=58).

3.5.6 Modelling CIRG and movement speeds

We calculated the means of all covariates within each adult female reindeer individual 95 % a-LoCoH home range for each sub-period. Linear mixed effect models were used to model access to high quality forage (CIRG) and movement variation (SD of movement rate) in reindeer as a function of brown bear density. Candidate predictors included bear density index, subperiod (calving and post-calving), elevation (m a.s.l.), terrain ruggedness index, slope (degrees), northness (relative aspect), reindeer herding district habitat type (mountain or forest), minimum distances to power lines, railways and large and small roads (all in m), the interaction between subperiod and bear density index, and year and individual id as random factor. Mean daily movement speed of reindeer was modelled with the same set of predictors, but with Julian day instead of study period, and using generalized additive models (GAM) with package “mgcv” (Wood 2011). Final models was determined with AIC.

4 Results and discussion

4.1 Brown bear predation on reindeer calves

Documentation of brown bear predation on the calving ranges of Udtja and Gällivare herding districts in paper I showed that brown bears killed mainly calves (333 out of 350 recovered reindeer carcasses documented killed by a radio-collared bear). Bears killed on average 11 calves on the calving ranges per season. Calf predation was mainly concentrated to three weeks in late May and the beginning of June (Fig. 4). This pattern was highly correlated with the abundance of new-born reindeer calves (e.g. Ropstad 2000, Holand et al. 2003), and is in accordance with previous documentation of predation on caribou (Adams *et al.* 1995; Jenkins & Barten 2005) and moose (Swenson *et al.* 2007). Reindeer calves rapidly increase mobility and locomotive ability (Lent 1974), and this is probably the main explanation for that predation is highly concentrated to the first weeks post-partum (Lent 1974; Jenkins & Barten 2005). Also, predation happened more frequently during nighttime (6 pm - 6 am), than daytime (6 am - 6 pm).

Seasonal kill rate did not differ between the demographic categories of bears when controlling for time spent on the calving grounds, except for females with cubs of the year, which were not documented to kill any calves. This differs from earlier studies on bears and other carnivores where demography influenced kill rates (Young & McCabe 1997; Knopff *et al.* 2010; Mattison *et al.* 2011). However, Boertje et al. (1988) did not document differences in kill rate on caribou calves between demographic categories of bears. Perhaps, when the bear is on the calving ground, the effect of high availability of vulnerable prey during a very short time override any effects of demographic differences on kill rates. Nevertheless, a large variation in kill rates within the categories, combined with a relatively small sample size can

explain the lack of difference in our study. One possible explanation for the variation independent of category could be that bears not necessarily adjusted home ranges to calf availability. Since calving locations differed somewhat between years, availability within the home range would change, and thus affecting kill rates.

Overall, seasonal kill rate was a positive function of time spent inside the calving ranges. Males, however, stayed on the calving ranges on average half as long as females. Males generally have larger home ranges than females (Dahle & Swenson 2003b) and also possibly move more during the mating season in May and June (Dahle & Swenson 2003a). The seasonal kill rate of adult males could thus have been underestimated in this study if their larger home ranges overlapped with calving ranges not included in this study.

Sub-adult bears had larger kill intervals than adult bears, and length of intervals increased slightly throughout the season. Sub-adults probably have less experienced than adults in hunting calves, which has been seen in other carnivores (Holekamp *et al.* 1997; Sand *et al.* 2006). An explanation to why kill intervals increased with time could be that calves get more difficult to catch as they grow. Also, lower densities later in the season can play a role.

The total number of bears potentially residing within the two study areas was estimated to be 71 [62-96] bears in Udtja and 58 [53-75] bears in Gällivare. Multiplying average bear seasonal kill rate, extracted from the model, with the total number of bears (excluding females with cubs of the year) indicated that brown bears were responsible for a considerable proportion (39 and 67 %) of the observed calf losses within the two reindeer herding districts. Average annual calf mortality in the herding districts was approximately 43 and 41 %, indicating that total bear caused mortality was around 29 and 16 %, in Udtja and Gällivare, respectively.

In a management perspective, the short window of predation is an important finding. This imply use of interventions that separate bears and calving reindeer in space and time during this short period. Also, that time on the calving ground seemed to be more important than differences between demographic categories, imply that generally reducing bear densities on the calving grounds likely will reduce predation rates on reindeer calves.

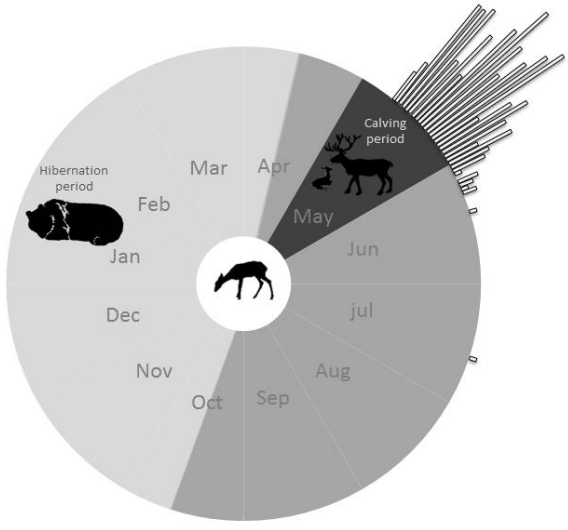

Figure 4. Timing and frequency of predation on reindeer neonates by GPS-collared brown bears in Udtja and Gällivare reindeer herding districts reported in paper I

4.2 Reindeer and brown bear resource selection and kill site spatial distribution

Estimation of reindeer and brown bear resource selection functions in paper II revealed marked differences in habitat selection between forest-living female reindeer and brown bears on the calving grounds. Reindeer mainly selected open areas and recent clear-cuts, and avoided young forest throughout the study period. Further, reindeer switched from selecting coniferous lichen forest and old clear-cuts in the predation period to selection of wetlands in the post-predation period. Brown bears mainly selected moss forest, young forest and avoided recent clear-cuts throughout the study period. However, reindeer did not seem to alter their behavior in response to spatiotemporal variations in the risk from brown bear predation. Rather, the results indicated that spatiotemporal behavioral adjustments by brown bears dominated, with a marked increase in spatial overlap between reindeer and brown bears in the predation period (versus post-predation period) and in high predation hours (versus low predation hours) (Fig. 5). The increased preference for reindeer habitat by brown bears was reflected in a distinct seasonal switch from

selection of less rugged terrain and higher elevations in the predation period to more rugged terrain, and lower elevations in the post-predation period, this being particularly pronounce in Udtja. Also, brown bear land cover selection was generally more similar to reindeer in the predation period. Reindeer habitat selection was nearly constant between high and low predation hours. In contrast, brown bears changed patterns in land cover selection at the daily level, more closely resembling reindeer in high compared to low predation hours. This suggest that bears might have actively searched for reindeer calves in our study areas. A comparable predator to the brown bear, black bears in North America, hunted in an opportunistic manner on caribou neonates (Bastille-Rousseau *et al.* 2011). Forest-dwelling woodland caribou are assumed to persist at low population densities and avoid predation by scattering out in the forest to reduce hunting efficiency by the predator (Bergerud & Page 1987; Seip 1991). The higher population densities in semi-domesticated reindeer herds, likely reduce the efficiency of such a spreading out strategy, and likely make active searching by the bears more profitable.

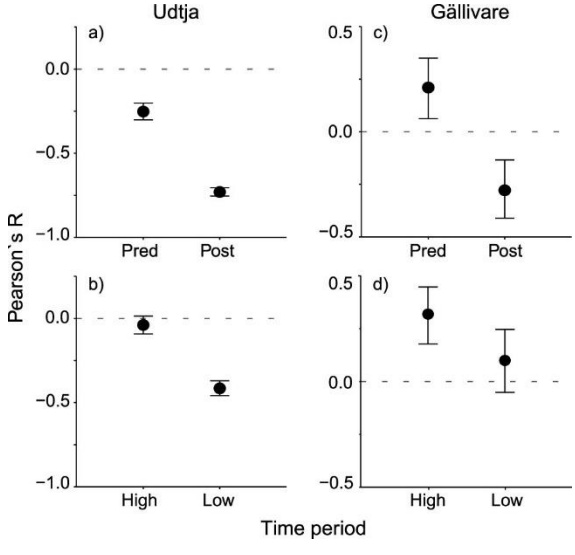

Figure 5. From paper II. Resource selection correlation between reindeer and brown bears, tested with Pearson's product-moment correlation, comparing the predation (Pred) and post-predation (Post) period, and high (High) and low (Low) predation hours, in Udtja reindeer herding district (a,b) and Gällivare reindeer herding district (c,d). The figure shows correlation coefficients (Pearson's R) and 95% confidence intervals.

The picture above was nuanced by relating calf kill sites to landscape characteristics and reindeer and brown bear resource selection functions in paper III. Comparing kill site spatial distribution to the relative probability of reindeer selection indicated that reindeer females might be able to take advantage of higher elevations in the landscape and to some degree areas closer to large roads, to reduce predation risk. Also, reindeer seemed to be at higher risk of encountering a brown bear and fall victim to predation in coniferous and young forest, and open habitat in Udtja, compared to wetlands. Moreover, the results suggested that the location of kill sites varied as a function of landscape characteristics (Fig. 6), and that this variation highly corresponded to reindeer – brown bear co-occurrence. However, we found possible evidence for a lower risk of kill in clear-cut habitats relative to co-occurrence probability in Gällivare and, despite increased co-occurrence probability close to roads during nighttime, that kill risk was unrelated to road distance in Udtja.

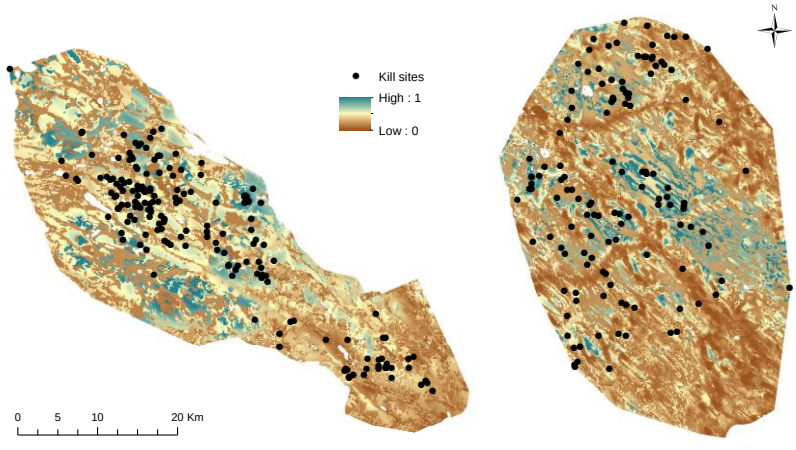

Figure 6. Reindeer calf kill sites used in the analysis in paper III, and relative probability of kill site occurrence, estimated from binomial logistic regression, comparing spatial attributes of kill sites to complete random locations within the study areas.

We suggest that the discrepancy between kill sites and co-occurrence probability close to small roads may be explained by variable road response between females with and without calf at heel, or lower hunting effort closer to roads by brown bears, rather than landscape effects. Reproductive status can affect behavior, and females with calves often express stronger avoidance responses than females without a calf (Wolfe, Griffith & Wolfe 2000; Barten, Bowyer & Jenkins 2001; Hamel & Côté 2007; Skarin & Åhman 2014; Leblond

et al. 2016). Females without calves could have been present, due to variation in timing of birth, and mortality throughout the season. Higher road use by bears in nighttime could reflect use of roads for travelling, and a higher activity level and movement rate by brown bears to compensate for less daytime activity, in response to diurnal variation in human activity (Ordiz *et al.* 2014).

Although brown bears generally increased preference for higher elevations in the predation period, bears may avoid ridge tops, to be less exposed. Thus, use of higher elevations by reindeer may reduce encounter risk, increase detection rates of brown bears and facilitate escape probability. Also, selection for clear-cuts may reduce bear encounter rates, provide good visibility and also, concealment cover for the calf (Dussault *et al.* 2012). Possibility for early detection of predators and hiding cover may reduce calf predation risk, as has been suggested both for caribou (Gustine *et al.* 2006; Carr, Rodgers & Walshe 2010; Pinard *et al.* 2012) and moose (Bowyer *et al.* 1999).

Both brown bear habitat selection patterns documented in paper II and the analysis of kill site distribution in paper III, suggested higher bear encounter probability and predation risk in young forest habitats. Clear-cut habitats may be beneficial in terms of calf survival, but logging activity will in eventually lead to greater abundance of young regenerating forest. Thus, forestry may in the long run reduce available reindeer habitats, but increase habitat preferred by brown bears. Also, as suggested by Dussault et al. (2012), if females retain high calving site fidelity and the selection for clear-cut areas persist as the forest grow, this can give adverse effects on survival. Indeed, calving site fidelity appear to be common among several ungulate populations (Ferguson & Elkie 2004; Wittmer, McLellan & Hovey 2006; Tremblay, Solberg & Sæther 2007).

Opposed to Gällivare, there were no indications of effects of clear-cuts on kill site distribution after accounting for co-occurrence probability in Udtja (i.e. no significant effects in the co-occurrence model). This may have been due to low occurrence of clear-cuts, especially recent clear-cuts, compared to Gällivare. Also, in Udtja kill site distribution relative to elevation, did not differ from that expected from reindeer selection. We wonder, however, whether an effect of elevation could have been masked by the elevation gradient that reindeer follow during spring, which is most pronounced in Udtja. Overall, the choice to pool data over years provide more robust estimates from a larger sample size, but may come at the cost of losing some information. Thus, future studies would benefit from using longer time series with the possibility to integrate climatic variation between years. Moreover, spatial variation in predation risk and antipredator responses can take place at a number of spatial

scale, and for example investigations of calving site selection and vigilance behavior should further improve our understanding of these systems.

4.3 Kill site fine scale characteristics

The majority of kill and control sites included in the fine-scale analysis in paper III, were located inside the forest with no visible edge. Yet, compared to control sites, kills occurred more frequently close to habitat edges (0-10 m), the majority being forest edges, and tended to occur less frequently at distances of 11-50 m from a visible edge (Fig. 7). The higher kill frequency close to edges could be because reindeer select such habitats for foraging, as they can provide nutrient-rich forage in spring (Warenberg 1982). However, forest edges may also reduce the probability of detecting brown bears coming from the forest. Thus, such habitats may represent a trade-off situation for reindeer, representing both high forage quality and high risk. In addition, edges may act as obstacles for movement and increase the predators chance to catch a calf that is trying to flee.

There was a slightly significant lower sightability (range finder measure) at kill sites compared to control sites (β=-0.016, 95% CI = [-0.032,-0.001]). This is in accordance with several other studies which have found that sightability plays a role for predation risk on ungulate calves (Bowyer et al. 1999, Gustine et al. 2006). There was also significantly less snow cover on kill sites compared to control sites (β=-0.05, 95% CI = [-0.09,-0.01]). We believe, however, that this most likely reflects reindeer`s preference for less snow cover. Importantly though, a bear might want to drag a kill out of deep snow or into cover, likely influencing these measures. Including field measurements of calving sites would clearly improve understanding of fine scale habitat characteristics and risk. Whereas several reports exist from North America (e.g. Gustine et al. 2006, Carr et al. 2010), data on reindeer calving sites in Fennoscandia is still scarce.

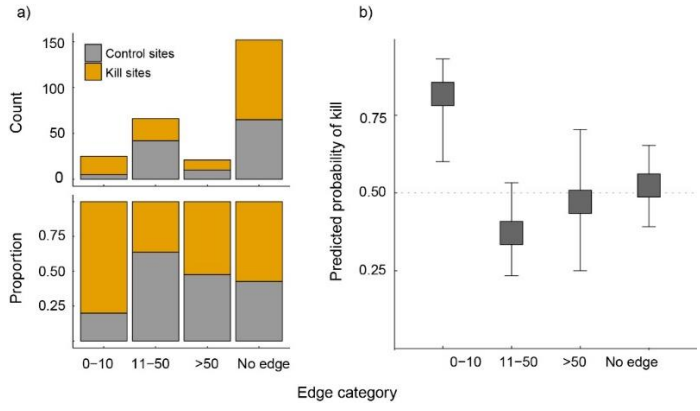

Figure 7. From paper III, showing a) data distribution between distance (m) to edge-categories for kill sites and control sites and b) predicted probability of kill compared to control sites given distance to edge category estimated from binomial generalized linear regression

4.4 The green-wave and brown bear density

In paper IV, we found that semi-domesticated reindeer followed movement paths with lower access to high quality forage when bear density was high, and generally moved faster at higher bear densities (Fig. 8). Our results thus indicated that predation risk limited reindeer's ability to follow the spring flush of nutritious forage, causing a trade-off between access to forage and avoiding predation. Nutritional demands, and availability of high quality forage, is generally assumed to be high during the ungulate lactation period (McEwan & Whitehead 1972; Crête *et al.* 1993; Parker, Barboza & Gillingham 2009). However, since *Rangifer* is recognized as a capital breeder (Taillon, Barboza & Côté 2013), largely relying on body reserves for gestation and early lactation (Stephens *et al.* 2009; Albon *et al.* 2017), they may be adapted to handle low forage quality at this time, and hence more willing to sacrifice following green-up in order to increase safety. Higher movement speeds at higher bear densities, may be due to more frequent flight responses due to bear encounters. To be on the move may also work as an antipredator strategy, to get less predictable in space (Lima & Dill 1990; Fischhoff *et al.* 2007). A simultaneous drop in movement speed across all populations towards the middle of the calving period, indicate the calving events (Panzacchi et al. 2013). Birth synchrony may also reduce predation risk (Rutberg 1987; Kerby & Post 2013).

Opposite to what we expected, the effects of bear density on green-up response and movement speed remained throughout the growth season. This could indicate a persistent response to risk by reindeer females, as has been shown for other ungulates (Byers 1997). However, both Barten *et al.* (2001)

and Latombe *et al*. (2013) have showed that caribou change habitat selection in response to temporal variation predation risk. An alternative explanation could be that effects from insect harassment was confounded with bear density during the post-calving period. The most alpine habitats, Sirges and Handölsdalen, also had the lowest bear densities reported in our study. Disturbance from insects can cause, or enhance, mismatch with green-up (Hagemoen & Reimers 2002; Bergerud & Luttich 2003; Skarin *et al.* 2010), but this effect may be less pronounced in alpine than in forest habitats (Helle & Aspi 1984).

Variation in movement rates was not affected by bear density. However, both movement speed and variation in speed was markedly higher in the forest, compared to in the mountains. This could be because brown bear predation generally is higher in forest herding districts, with the brown bear home ranges completely overlapping the calving grounds. Forest reindeer could be driven to move more between smaller patches of forage- and cover habitats to hide from predators (Mysterud & Østbye 1999), and frequently increase their speed to flee from bears. Reduced intake of high quality forage combined with higher and more variable speed, affects the energy budget, and is expected to have negative effects on body condition (Couturier *et al.* 2009; Bischof *et al.* 2012). Overall, our study thus indicates that the presence of brown bears may have indirect costs for the reindeer females and their calves.

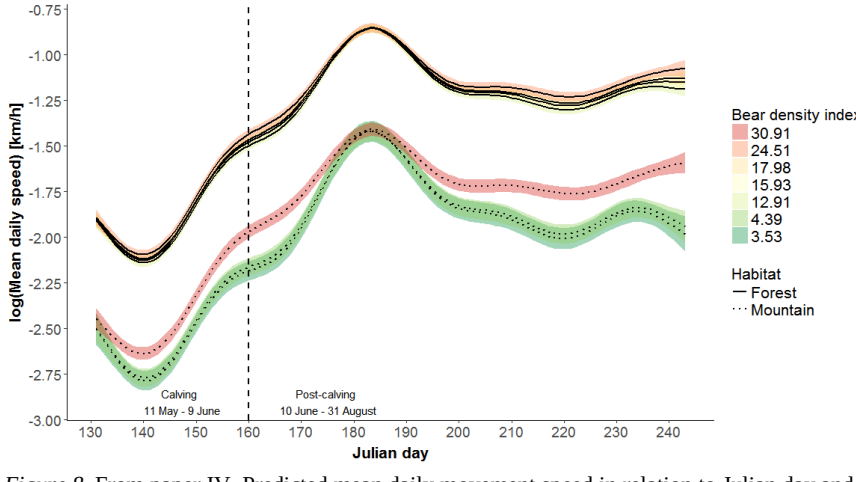

Figure 8. From paper IV. Predicted mean daily movement speed in relation to Julian day and bear density index, based on a generalized additive model. Predictions are made for the mean bear density experienced by all individuals within each herding district. The herding district habitat is shown with solid (forested) and dashed (mountainous) lines. The vertical dashed line shows the two sub-periods calving (11 May - 9 June) and post-calving (10 June - 31 August).

5 Concluding remarks

Even though brown bears are known to be efficient predators on ungulate neonates (Adams *et al.* 1995; Linnell *et al.* 1995), only a few studies have documented brown bear predation on semi-domesticated reindeer calves in Fennoscandia (Nieminen 2010). In paper I in this thesis, we documented high predation rates by brown bears on semi-domesticated reindeer calves. That reindeer calves mainly are vulnerable to brown bear predation during the first weeks post-partum, is in accordance with previous findings (Adams *et al.* 1995; Linnell *et al.* 1995). In fact, in the Sámi language reindeer neonates less than two weeks old are traditionally called "njäbttso", which means weak and with poor locomotive skills (Ryd 2007), indicating that these are recognized as important and closely linked attributes of the calf.

Reindeer herders in Sweden are compensated for potential losses to brown bear predation based on the size of their herding district (www.sametinget.se). This differs from compensation for losses to the other large carnivores, which are based on number of individuals or reproducing pairs. The difference is due to both infrequent inventories and lack of knowledge of kill rates from brown bears, but results in inadequate compensation for herding districts with high brown bear predation. Thus, for the compensation system to work better, well-founded data on both the occurrence of brown bears and the expected losses and indirect costs are required. Overall, the high bear predation rates on reindeer calves reported in paper I suggest that brown bear predation cause considerable higher costs than what is previously been accounted for in Sweden (Karlsson *et al.* 2012). The baseline data on brown bear kill rates and timing of predation reported here can thus contribute significantly to improved predictions of the losses to predation caused by brown bears, and also, to better finding and evaluating possible mitigation actions.

Forest reindeer herding districts are probably particularly vulnerable to brown bear predation, with their calving ranges completely overlapping with

the brown bear home ranges. The reindeer are also scattered out in smaller groups in the forest during calving making guarding more difficult, compared to mountain calving ranges. Furthermore, the higher densities in semi-domesticated reindeer herds, compared to forest-living wild reindeer and caribou, possibly make a space-out strategy to increase predator searching time less efficient, and active searching for reindeer calves by the brown bears more profitable, which may further increase vulnerability to predation. This shows the importance of well-grounded knowledge within different study systems.

In terms of altered resource selection on a daily and seasonal basis, brown bear behavioral adjustments to search for reindeer seemed to override, at least partly, antipredator responses by reindeer. Nevertheless, a closer investigation of kill site spatial distributions suggested that female reindeer might utilize clear-cuts, higher elevations and areas closer to roads to reduce risk from bear predation. The preference by brown bears for young forest may indicate that logging activity on the calving range can have negative consequences for the reindeer in the long term. To further consider how the magnitude and the spatial arrangements of logging influence the risk landscape on the calving range would add important knowledge in this respect. It would also be of interest to investigate the degree of calving site fidelity in semi-domesticated reindeer, and how patterns of fidelity are influenced by landscape change.

The broader scale examination of female reindeer movements indicated that behavioral responses to brown bear presence come at a cost of forage acquisition. It is interesting that there were generally few signs of adjustments to temporal variation in risk, though it has been documented in other *Rangifer* systems (Barten *et al.* 2001; Latombe *et al.* 2013). Overall, deviations from optimal foraging and increased movement rates, can lead to poorer body condition and have negative consequences for population dynamics. The results underline that indirect effects of carnivore presence should also be considered when evaluating the total costs from predation, as has been suggested in recent years across a broad range of ecosystems (Lima 1998; Brown & Kotler 2004; Creel *et al.* 2007; Zanette *et al.* 2011).

To enable co-existence of viable large carnivore populations and a sustainable reindeer husbandry in Fennoscandia, the human-wildlife conflict level needs to be reduced. In 2013, the Sami Parliament and the Environmental Protection Agency in Sweden agreed on a "tolerance level" for maximum acceptable reindeer loss due to predation. It has however proved challenging to apply this in practical management, mainly due to a lack of trust and common knowledge base. Finding agreements on this, combined with development of compensations schemes that better reflects the true costs of presence of

predators, will hopefully facilitate the co-existence of reindeer husbandry and large carnivores.

Moreover, the main challenges experienced by reindeer husbandry today arise from increasing predator populations and land use changes on the reindeer ranges, e.g. growing infrastructure development and forestry activities (Pape & Löffler 2012). Thus, future work needs to integrate the combined costs from predators, human encroachment, and also climate variations, on reindeer herd productivity and the lives and economy of the herders. A solid knowledge base is necessary in order to sustain a viable reindeer husbandry and mitigate disputes with conflicting interests in the reindeer herding area.

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